MORPHOLOGY AND STRATIGRAPHIC RANGE OF THE PHYLLOCARID CRUSTACEAN *CARYOCARIS* FROM ALASKA AND THE GREAT BASIN

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ABSTRACT. Exceptionally well-preserved specimens of *Caryocaris* from Alaska and the Great Basin show a peculiar shell enrolment; several other important skeletal details are described for the first time. In the light of this new material, Ruedemann's types that are the basis for his reconstructions of *Caryocaris* are re-examined. Finally, a review of the stratigraphic range of *Caryocaris* leads to the conclusion that none of its reported Silurian species are definitely *Caryocaris*. The range of the genus should therefore be restricted for the present to the Ordovician and probably to the lower half of the system.

SINCE Salter (1863) named *Caryocaris*, a pod-shaped crustacean from the Skiddaw Slates of the Lake District, England, it has been reported from Ordovician graptolitic shales in North America (Gurley 1896; Ruedemann 1921), South America (Bulman 1931), Australia (Chapman 1903), and Scandinavia (Størmer 1937), and new species of *Caryocaris* have been described from Silurian graptolitic shales in south-eastern Alaska (Ruedemann 1934) and Oklahoma (Ruedemann 1935). The flattened and crushed specimens hitherto described are difficult to interpret and have resulted in a number of different restorations.

The purpose of this paper is to describe exceptionally well-preserved specimens of *Caryocaris* from Alaska and Nevada that show for the first time a peculiar shell enrollment and several morphological details. In the light of this new material, Ruedemann's types that have served as the basis for his classical reconstructions are re-examined, and, finally, the stratigraphic range of *Caryocaris* is reviewed and greatly reduced.

Acknowledgements. This study is the result of the discovery of exceptionally well-preserved *Caryocaris* in mapping the Charley River (1:250,000) and Eagle D-1 (1:63,360) quadrangles in east-central Alaska (Brabb and Churkin 1964, 1965). I am indebted to Earl E. Brabb (U.S. Geological Survey) for his interest and numerous useful suggestions; to W. D. Ian Rolfe (Hunterian Museum, Glasgow) for critically reading the manuscript; to J. Wyatt Durham (University of California, Berkeley) for suggesting shell enrollment to explain the spirally coiled carapaces; to Copeland MacClintock (Peabody Museum of Natural History) for ideas concerning shell wall microstructure; to Robert A. Gulbrandsen (U.S. Geological Survey) for interpreting the X-ray patterns of *Caryocaris* shell material; to Charles W. Merriam (U.S. Geological Survey) for kindly furnishing his collections of *Caryocaris* from Nevada; to A. R. Palmer (U.S. Geological Survey) for arranging loans of type specimens from the U.S. National Museum; and to Donald W. Fisher and Clinton F. Kilfoyle (New York State Museum) for loaning type specimens in their care. Publication is authorized by the Director, U.S. Geological Survey.

CARYOCARIS IN EAST-CENTRAL ALASKA

Caryocaris occurs in several graptolitic shale horizons of Ordovician age in the Road River Formation (Ordovician and Silurian) of east-central Alaska and is especially

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abundant in chert at the base of the formation (Churkin and Brabb 1965). The best preserved specimens described below were obtained from loc. M1001-CO (see Appendix) near the Alaska–Canada border. Here abundant specimens of *Caryocaris* are preserved with the graptolites *Isograptus forcipiformis*, *Isograptus caduceus* cf. var. *maximodivergens*, and *Didymograptus* cf. *D. nitidus* in a greyish-black chert 5 to 8 feet stratigraphically above unnamed limestone containing Late Cambrian trilobites. Both *Caryocaris* and the graptolites are preserved in relief and are easily distinguished by their phosphate bloom, apparently a white phosphatic-weathering product (Pl. 64, figs. 1, 2). The graptolites associated with the *Caryocaris* indicate a latest Arenig or earliest Llanvirn age equivalent to graptolite Zone 5 of *Didymograptus hirundo* or Zone 6 of *Didymograptus bifidus* of Elles and Wood (1901–18). Conodonts found in chert directly below the *Caryocaris* locality were identified by John W. Huddle, of the U.S. Geological Survey, and suggest late Arenig. Thus, all of the Tremadoc and most of the Arenig seem to be absent in the less than 5-foot chert interval between the conodont locality, the lowest fauna in the Road River Formation, and the highest trilobite collection from the underlying Cambrian limestone. At loc. 63ACn 1533, about 3 miles east of loc. M1001-CO, *Caryocaris* is again very abundant in the basal Road River Formation, where it occurs in thin beds of chert pebble conglomerate and chert grit interstratified with and cemented by dark-grey chert. The poorly sorted angular grains, cross-laminae, and scour-and-fill structures suggest that the *Caryocaris* material, in places reaching coquinoid proportions, was laid down in a high energy environment as part of a basal deposit unconformably overstepping Cambrian limestone.

MORPHOLOGICAL FEATURES OF *CARYOCARIS* IN EAST-CENTRAL ALASKA

The Alaskan specimens of *Caryocaris* are unusual in that they have in various degrees their third dimension preserved in chert instead of appearing as completely flattened films in shale. Because the Alaskan specimens are not completely flattened, they reveal a peculiar spiral coiling of the carapace wall here described for the first time. In addition, other important skeletal features hitherto unknown or inadequately figured are described below, and lastly the microstructure and composition of the carapace wall are discussed. The terminology of the exoskeletal elements of *Caryocaris* has not been standardized, and therefore the nomenclature used in the following description is given in text-fig. 1.

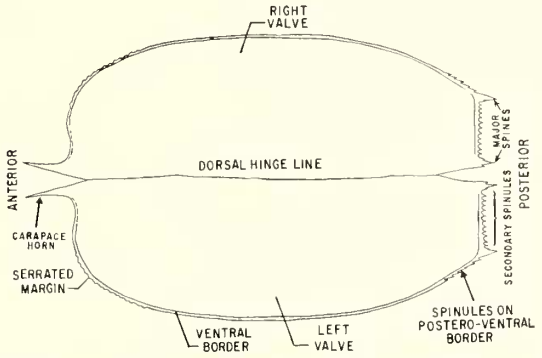
Carapace enrolment. Spirally coiled carapaces of *Caryocaris* appear in long view as cylindrically-shaped body walls tapering to blunt points at each end (Pl. 64, figs. 3, 4). All the larger specimens were partially broken, but several are still nearly 20 mm. long. Their corresponding diameters are about 2 mm.; and width to length ratio is about 1 : 10 as contrasted with about 1 : 4 in associated flattened specimens.

In a number of specimens transverse breaks show in cross-section the internal spiral coiling of the carapace wall (Pl. 64, figs. 5, 6). The fragile carapace walls, nearly black in colour, are supported by microcrystalline white quartz deposited between each whorl. In thin sections random profiles through coiled carapaces reveal a number of differently appearing patterns of the shell wall (Pl. 64, fig. 7) of which the shapes of the longitudinal (Pl. 64, fig. 8) and nearly transverse profiles (Pl. 65, fig. 1) are highly characteristic.

Apparently each coiled piece is a single valve that is the result of separation, perhaps by moulting, along the dorsal hinge line followed by in-curling of the valve wall starting from the ventral margin.

Spined posterior margin. Ruedemann (1921) originally described several features of *Caryocaris* from graptolitic shale here referred to the Road River Formation at the Alaska–Yukon boundary, but the coiled and three-dimensional specimens preserved in chert from the base of the formation apparently were not available to him.

'The Alaska–Yukon material', Ruedemann wrote, 'which is not obscured by an imperfect cleavage leaves no doubt that the posterior margin of the carapace was indeed furnished with a fine comb of uniform bristles or teeth.' As Ruedemann pointed out, the



TEXT-FIG. 1. Orientation and terminology of *Caryocaris* used in this paper.

posterior margins of the Alaska–Yukon species certainly have a row of 'bristles or teeth' (here referred to as spines and spinules to divorce these structures of unproved function from a genetic connotation) and are not a product of structural deformation. These spines, however, are not of equal size as Ruedemann claimed. The spine at each end of the posterior margin is several times larger than the 13 intervening spinules (Pl. 65, fig. 3). In addition, the ventral margin in its posterior portion, has a row of 5 and possibly more posteriorly directed spinules (Pl. 64, fig. 3 and Pl. 65, fig. 3) which have not been previously recorded anywhere and are rarely preserved even in the best Alaskan specimens.

Carapace horn. The Alaskan *Caryocaris* certainly has a horn-like projection at the anterior end of its dorsal margin (Pl. 65, fig. 2) but it is simply a prolongation of the carapace wall instead of a 'distinct plate' or true rostrum as Ruedemann (1921, p. 96, figs. 45, 51; p. 99) indicated.

Segmentation and appendages. Although the Alaskan collections consist of several hundred specimens, none of the carapaces has either an abdomen or telson attached as Ruedemann (1921) showed in figs. 46, 48, and 51. Several fragments that resemble 'abdomina' and 'telsons', were found but these segmented structures, though they are well preserved, are completely detached from any carapace and their biological affinities to *Caryocaris* can only be conjectured. An examination of the original specimens in the New York State Museum from which Ruedemann's figs. 46, 48, and 49 were drawn has

also failed to show any justification for the segmentation or appendages shown in his drawings.

Ventral margin. The ventral margins of the Alaskan *Caryocaris* have a thickened border that is more or less well preserved. In flattened specimens this border is frequently impressed in various positions on the opposite valve wall, thus suggesting that the carapace walls were in these cases enrolled before flattening.

Carapace surface ornamentation and wall microstructure. The surface of the *Caryocaris* exoskeleton has the iridescent lustre common to other phosphatic shells and appears smooth except in flattened specimens from shale, where it is generally finely wrinkled. Under the microscope, however, the exterior of the carapace is seen to be distinctly corrugated into very fine furrows and ridges that form a slightly sinuous pattern.

The microstructure of the carapace wall in thin section consists of three distinct layers (Pl. 64, fig. 7; Pl. 65, fig. 1). The outer and inner layers range in colour from pale yellowish-orange to shades of yellowish-brown and are separated from each other by a much thinner middle layer that is dark brown. Frequently the edges or centre of this middle layer of the carapace wall serve as a plane along which the inner layer separates from the outer layer. A very faint fibrous structure (possibly representing in part very fine canals) normal to the carapace wall can be seen in the inner and outer layers, but the middle layer instead seems to have a faint lamination or parting, especially along its centre, that parallels the carapace layering. Several specimens seem to have a very narrow hollow space where two carapace walls come to a point. Presumably this is the union of two valves along the hinge line.

In thin sections the shells have the faint birefringence of microcrystalline apatite that probably represents very nearly the original chitino-phosphatic material of the exoskeleton. The mineralogical composition of *Caryocaris* shell material separated out from Coll. 63ACn 1533 gave the X-ray pattern of carbonate-fluorapatite.

Involute phosphatic shells similar to those described above but only one-third normal

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EXPLANATION OF PLATE 64

Fig. 1. Crushed carapaces of *Caryocaris curvilata* associated with *Isograptus caduceus* cf. var. *maximodivergens*. The phosphatic fossils weather greyish-white and stand out clearly against the greyish-black chert matrix; USNM 147441, loc. M1001-CO, Road River Formation, east-central Alaska. ×2.

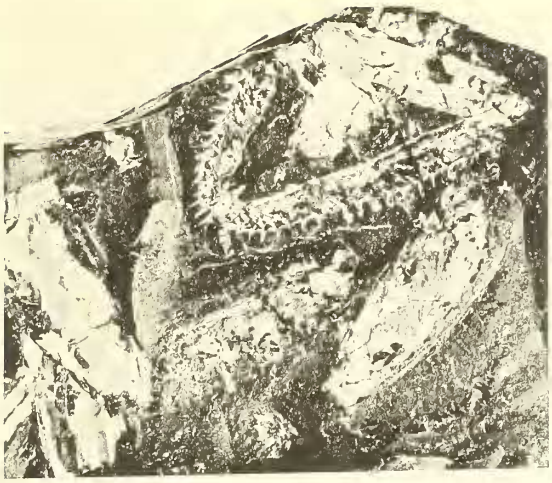
Fig. 2. Right valve view of *Caryocaris curvilata* associated in the same chert fragment with *Isograptus forcipiformis*; USNM 147442, loc. M1001-CO, Road River Formation, east-central Alaska. ×2.

Fig. 3. Enrolled valve of *Caryocaris* (lower centre) next to two partially flattened valves. The valve in the upper left corner shows the spined posterior margin characteristic of *Caryocaris curvilata* and the rarely preserved fine spinules along the postero-ventral border; USNM 147443, loc. M1001-CO, Road River Formation, east-central Alaska. ×3. Photographed with ammonium chloride coating.

Fig. 4. Enrolled *Caryocaris* reflecting light from its phosphatic carapace that has an iridescent lustre; USNM 147444, loc. M1006-CO, Road River Formation, east-central Alaska. ×2.

Figs. 5, 6. Enrolled *Caryocaris* showing transverse views of the spiral coiling of the very thin and dark carapace wall. The delicate spiral structure is supported by white microcrystalline quartz filling the space between each whorl; 5, USNM 147445; 6, USNM 147446; loc. M1001-CO, Road River Formation, east-central Alaska. ×6.

Figs. 7, 8. Photomicrographs of a thin section through coiled carapaces of *Caryocaris*; 7, random cross-section across a partially crushed specimen showing a complicated pattern of carapace wall folding and the characteristic three-layered microstructure of the carapace wall, ×114; 8, longitudinal profile, ×45; USNM 147447, loc. 63ACn 1533, Road River Formation, east-central Alaska.



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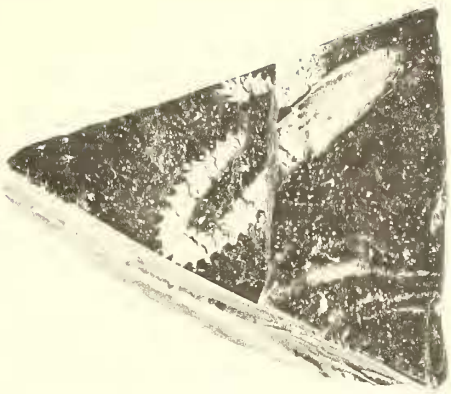

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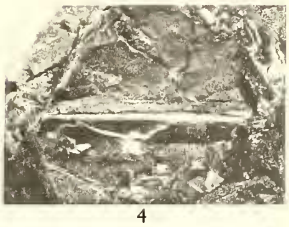

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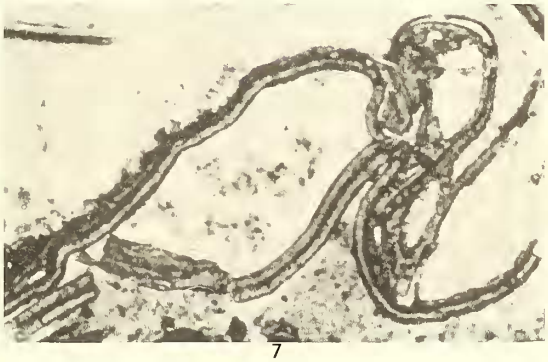

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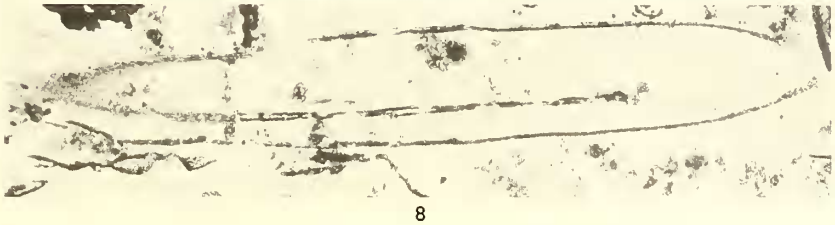

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size (Pl. 65, figs. 4–6) were found in chert grit layers of the basal Road River Formation near the Yukon River (loc. 63ABa 3181B). Fig. 6 shows that the shell wall has the same three-layered microstructure as in *Caryocaris*. In the heart-shaped cross-sections there is a very narrow but definite break in the shell microstructure where the shell wall comes to a point, and this suture probably represents the dorsal hinge line. The shell walls coiled into a double spiral can then be interpreted as two connected valves curled in along their ventral margins. In some cross-sections the incurled valves on either side of the supposed dorsal hinge line have shell walls of variable and unequal thickness but this is largely due to splitting of the layered walls, as in the feather edge of the outer whorl in fig. 6, rather than because of any original difference between the two valves.

Mertie (1930, pl. 9) illustrated involute shells from cherty grit in the same area. Edwin Kirk (*in* Mertie 1930, p. 83) wrote that 'the zoological affinities of these curious fossils are doubtful' and assigned them to the Pteropoda 'mainly by a process of elimination'. These involute fossils reported by Mertie appear in thin section identical to those in Plate 65, figs. 4–6, and in both cases are similar in outline and have the same shell wall microstructure as those of *Caryocaris* described above.

MORPHOLOGICAL FEATURES OF *CARYOCARIS* FROM NEVADA AND IDAHO

Gurley (1896) described *Caryocaris wrightii* Salter and named a new species, *C. curvilatus*, from Summit, Nevada (this locality lies in what is known today as Garden Pass). In a large collection of *Caryocaris*, made by C. W. Merriam from the same graptolitic shale at Summit, Nevada, I found several specimens of *C. curvilata* with a well-developed carapace horn not originally recognized by Gurley. In these specimens the posterior border, where preserved, is lined with a row of spinules. The larger spines at each end of the posterior border, although generally incompletely preserved in the Summit specimens, were recognized and figured by Gurley (pl. 5, fig. 3) but were not mentioned by Ruedemann (1921) in his subsequent description of *C. curvilata* from the Alaska–Yukon boundary. The type species of *Caryocaris* may lack the posterior spines and carapace horn so characteristic of the western North American species discussed in this paper, and as W. D. Ian Rolfe pointed out (*in* Theokritoff 1964, p. 183), *Caryocaris curvilata* and other species of *Caryocaris* in America may belong to *Rhinopterocaris* Chapman, a Lower Ordovician genus from Australia that has been synonymized with *Caryocaris* but perhaps is generically distinct.

The major differences in shell width as well as the 'complicated foldings and refoldings of the marginal filaments' reported by Gurley (1896, p. 87) along the ventral margin are probably a result of carapace enrollment before flattening as noted above in the Alaskan material. Now that specimens of *Caryocaris curvilata* from its type locality are known to have a carapace horn and a distinctively spined posterior margin, it may be concluded that the better-preserved Alaskan specimens are more certainly conspecific with *C. curvilata* from Summit, Nevada. The Alaskan specimens provide details not preserved in the type material from Nevada.

Several tridentate fossil parts resembling caudal appendages of various phyllocarids (Jones and Woodward 1888–99, pl. 10, figs. 10, 11; Ruedemann 1934, pl. 22, fig. 7) occur with *Caryocaris curvilata* at the Summit locality but in every case are detached from any

carapace. In this and in all collections of *Caryocaris* studied no single appendage was found attached to a carapace, nor was there evidence of body segmentation. Ruedemann (1921, p. 96, fig. 51) in a restoration of the *Caryocaris curvilata* from the Alaska–Yukon boundary connected a segmented 'abdomen' to a spined posterior margin and then attached a tridentate 'telson' to the end of the 'abdomen'. Later Ruedemann (1934, p. 92, pl. 22, figs. 8, 9) illustrated a specimen of *C. curvilata* from Trail Creek, Idaho, that he implied showed 'both the abdomen and the telson in place' for the first time. A re-examination of Ruedemann's plesiotypes indicated that his figs. 8 and 9 are actually a highly inferential reconstruction and that none of the specimens in the USNM type collection no. 90858 from Trail Creek loc. 1367 has a telson-like structure attached to the posterior end of a carapace as Ruedemann's figures show. According to W. D. Ian Rolfe, of the Hunterian Museum, Glasgow (written communication, May 1965), the original specimen from which Ruedemann's figs. 8 and 9 were made lacks the anterior part of the carapace including any 'articulated rostrum', and has a telson near the posterior end of the carapace, but definitely detached from it. Unfortunately, this specimen has been recently damaged and the posterior end of the carapace has been chipped off and lost, further obscuring any connexion between the carapace and the associated telson. Another and more completely preserved specimen (text-fig. 2*a*) on the same shale slab as the type for Ruedemann's figs. 8 and 9, has a tridentate structure that is probably part of another specimen adjoining its dorsal margin instead of being attached to the posterior end, and also lacks any definite articulated rostrum or segmented abdominal parts as indicated by Ruedemann.

In shales *Caryocaris* is generally preserved with either the right or left valve showing. Rarely are both valves found connected. Ruedemann (1934, pl. 22, fig. 5) illustrated such a specimen from Trail Creek, Idaho, and noticed 'prominent spines on the inner point of the posterior margins on both sides of the dorsal hinge'. He failed to mention, however, a correspondingly large spine at the opposite (ventral) end of the posterior margin of the left valve (see text-fig. 2*b*, a camera lucida drawing of Ruedemann's figured specimen). In the same collection from Trail Creek a specimen of *C. curvilata*

EXPLANATION OF PLATE 65

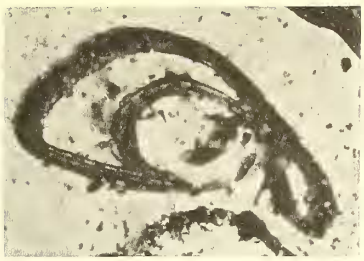
Fig. 1. Photomicrograph of nearly transverse cross-section through coiled valve of *Caryocaris*; USNM 147448, loc. 63ACn 1533, Road River Formation, east-central Alaska. ×86.

Fig. 2. Right valve view of small *Caryocaris* with part of its carapace horn still intact; USNM 147449, loc. M1001-CO, Road River Formation, east-central Alaska. ×5. Photographed with ammonium chloride coating.

Fig. 3. Close-up of the posterior portion of *Caryocaris curvilata* shown on Pl. 64, fig. 2. The two spines at each end of the posterior margin are separated from each other by 13 intervening spinules. The row of 5 posteriorly directed spinules along the postero-ventral margin is also preserved; USNM 147442, loc. M1001-CO, Road River Formation, east-central Alaska. ×10. Photographed with ammonium chloride coating.

Figs. 4–6. Photomicrographs of cross-sections of very small involute shells resembling *Caryocaris*. In the heart-shaped cross-sections there is a break in the shell wall where it comes to a point. 4, ×35; 5, ×70; 6, ×114. All in thin section USNM 147450, loc. 63ABa 3181B, Road River Formation, east-central Alaska.

Figs. 7–9. *Caryocaris curvilata* from shale at Ninemile Canyon, east-central Nevada; 7, left valve view of flattened specimen, USNM 147451, ×3; 8, anterior portion of carapace with the entire carapace horn intact, USNM 147452, ×3; 9, spined posterior margin, USNM 147453, ×10.



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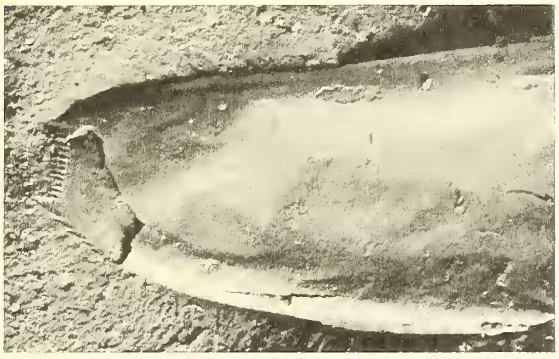

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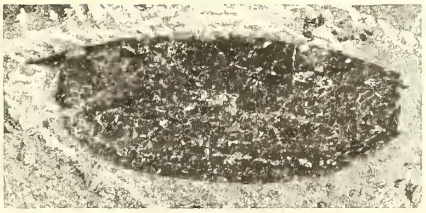

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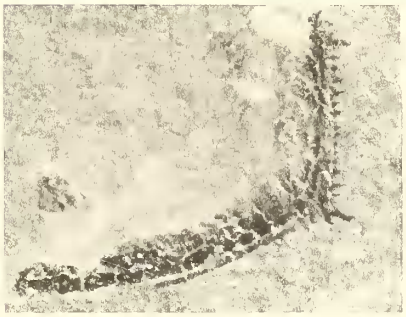

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